Dispatches

Group Behaviour: Leadership by Those in Need

A new model of animal group behaviour shows that, when the need to reach a target outweighs the costs of splitting from the group, a minority of the most 'needy' individuals become the leaders of large groups.

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As in much of biology, explaining the behaviour of animal groups can lead us in two different directions: the mechanistic and the functional [1]. Mechanistic explanations look at how animals interact to produce group level patterns. For example, how do starlings produce the spectacular evening displays without any central co-ordination? Functional explanations are based on arguments about why a behaviour has evolved through natural selection: starlings in a larger flock are less likely to be eaten if the flock is attacked by a hawk. Behaviours that improve an animal's chances of reproduction will increase in frequency in the population, and those with behaviours which are detrimental to survival will die out.

While mechanistic and functional approaches are complementary, they are often carried out in isolation from one another. Working largely independently of functionally-minded biologists, physicists and mathematicians have during the last 15 years studied the mechanisms underlying the behaviours of flocks of birds, shoals of fish and insect swarms. With their somehow regular, but at the same time unsymmetrical and dynamically-changing shapes, moving animal groups provide a prototypical example of a complex system. The question has been whether these shapes can be generated by individuals that interact locally with no global knowledge. The answer has been an emphatic 'yes'. The main theoretical tool in producing this answer are self-propelled particle models (Figure 1). These models describe animals as particles which respond to their local neighbours through repulsion, attraction and alignment. Simulations of the models have shown that simple local rules can produce directed motion of large groups [2,3], as well as more complex structures such as toroidal milling and confusion responses to predators [4].

These striking results have begun to influence biologists. Larissa Conradt and Tim Roper have written a series of papers about the functional costs and benefits of leading and following when making group decisions [5,6]. In a new paper in *American Naturalist* [7], they have teamed up with two specialists in the mechanistic approach, Jens Krause and Iain Couzin, to investigate how conflicts of interest influence the direction of group movement. They model a situation where groups consist of two types of individuals that prefer to go in opposite directions, but also want to remain together. They show that the degree of assertiveness individuals should exert for going in their preferred direction depends upon the cost of splitting and the benefit of going to your own preferred target. By tuning this assertiveness to reflect these costs and benefits, a small minority of individuals with a strong 'need' to go to their target can assert leadership over a larger majority of less-needy individuals. Group fragmentation is predicted to occur relatively rarely and only in cases when the benefits of staying together are small.

To those who have been studying mechanisms of collective motion these modelling results will come as no great surprise. The strength of Conradt *et al.*'s [7] paper, however, is that it makes the sort of predictions which relate to and can be tested in animals. For example, they predict that large groups will not be led by some socially dominant individuals, but rather by a small number of individuals which are most food deprived. Furthermore, exposing animals to predation risk or starvation should change their speed of movement, as well as their responsiveness to and distance to those around them.

While Conradt *et al.* [7] provide a good example of functionalists turning towards mechanism, it is less clear whether the mechanistic researchers will allow themselves to be led by function. The pages of

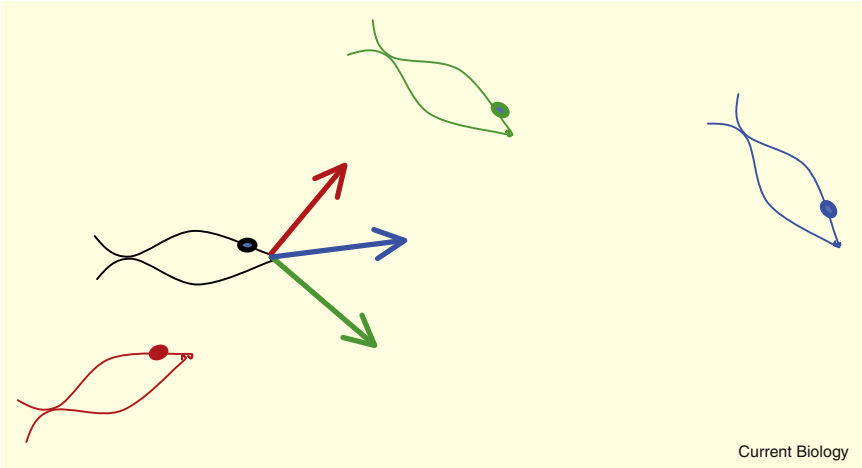

Figure 1. A schematic representation of the interactions in self-propelled particle models.
The fish-like objects represent particles and the vectors denote their respective directional influence on the focal particle (black). The focal particle is repulsed by the nearby red particle, aligns with the green particle and is attracted to the distant blue particle. Exactly how repulsion, alignment and attraction depend on the distance to neighbours varies from model to model, but typically very nearby particles have a repulsive force and further away particles are attractive and aligned to.

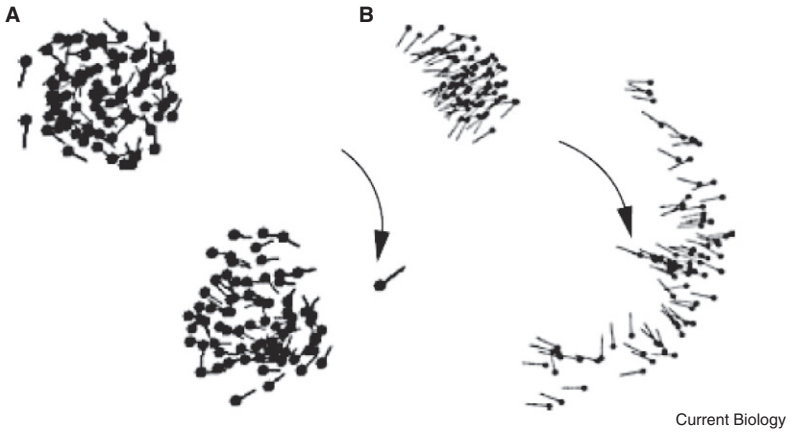

Figure 2. Typical example of the two types of evolutionarily stable flock types in the Wood and Ackland [15] model.

Each flock is shown before and during the attack of a predator. (A) is a compact milling torus that responds relatively slowly to the predator while (B) is a dynamic parallel group with a high degree of alignment but only loose between individual attraction. When a predator attacks, the group fans out to avoid it. Prey heads are marked with a circle and the line indicates their current velocity. Predators are larger and marked with an arrow. (Reproduced with permisssion from [15].)

engineering and physics journals are currently filling with articles on whether collective motion involves a first-order or second-order phase transition, the importance of different noise terms and links to control problems in robotics. While such articles certainly keep the minds of physicists busy and may well have future technological applications, they stretch far beyond what has been established empirically about the movement of real animal groups. In this respect we can take encouragement from Conradt *et al.* [7]. They have shown that a small determined group of functionally minded biologists can (in theory) lead the herd of theoreticians towards a better understanding of collective animal behaviour.

So where should we lead these theoreticians? The first big question lies in validating these elegant models of flocking. Everything I discuss above is a theoretical edifice, based on building the simplest possible models that reproduce patterns at the level of the group. With a few notable exceptions [8,9], there has been little work looking at how individual fish, birds and insects interact with each other within groups. Experimental work has instead concentrated on quantifying collective patterns, which in combination with modelling studies provide strong hints of what goes on at an individual level [10,11]. The goal of establishing the rules in terms of local attraction, repulsion and alignment for any particular species has yet to be achieved.

This goal is, however, in sight. Michelle Ballerini, Andrea Cavagna and a team of co-workers on the Starflag project [12,13] have recently performed three-dimensional reconstructions of starling flocks, allowing them to establish a better understanding of how individuals maintain their position relative to neighbours. Considering that it is one of the first projects of this type, it was possibly over-ambitious: filming thousands of starlings in natural conditions poses technical problems that would not arise in controlled laboratory situations with small numbers of individuals. Given the success of the project under difficult conditions, we can expect to see the techniques developed here to be applied to a variety of other species in the laboratory and field [14].

Until the data come through for mechanistic models of flocking there remain some interesting functionally driven theoretical challenges. Conradt *et al.* [7] do not investigate the evolutionary stability of strategies of individuals, and as such do not fully take the game theoretic approach adopted by functionalists. Here, a paper by Jamie Wood and Graeme Ackland [15] shows us the way. They looked at how the rules of motion of animals evolve under predation pressure. Over a number of generations they subjected self-propelled particles to predation by a fast moving predator particle, allowing only those which survived attack to pass their rules for interacting with neighbours on to future generations. They found that both local milling and fountain-like confusion effects arose from evolutionarily stable strategies in the rules individuals adopted under predation (Figure 2).

This approach of applying selection pressure to self-propelled particles could enhance our understanding of flocking. It may even reveal that different noise terms and the order of phase transitions are actually important from an evolutionary point of view [16]. So as we celebrate Darwin's 200th birthday I would urge those modelling flocking to think again about his very functional theory and how it might shape the spectacular shapes which animal groups produce.

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Cell Division: Breaking Up Is Easy to Do

How did cells divide before protein machines evolved? A new study shows that bacteria can reproduce without the division machinery, supporting the idea that primordial cells could have divided using physical mechanisms alone.

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Life is organized into cells that grow and divide. In addition to providing a semipermeable barrier and restricting diffusion, cellular organization would have been important during the origins of life to help prevent the rise of genetic 'parasites'. For example, a ligase ribozyme might catalyse production of a complementary copy of itself by stitching together two shorter RNAs, but it could also help produce unrelated, inactive molecules that benefit from the ribozyme's activity without contributing to the system. Compartmentalization into cells reduces this problem by keeping related molecules together, with cell division periodically purging the parasites [1,2]. Cell membranes might have formed spontaneously early on, because amphiphilic lipids readily self-assemble into liposomes in aqueous solution, and such molecules have been found in carbonaceous chondrite meteorites, whose composition is thought to resemble the early solar system [3]. In fact, organic extracts from the Murchison meteorite form cell-like boundary structures in water [4].

Primitive cells have been studied primarily through a bottom-up approach, in which minimal systems are built up from scratch, and chemical or physical forces used to achieve growth and division. For example, vesicles composed of fatty acids grow larger when given a fatty acid feedstock, such as micelles [5,6]. Although such systems are exceedingly simple compared with modern life, this approach has yielded surprising insights into prebiotic cellular dynamics. Even a simple form of competition can emerge among these model protocells, as osmotically swollen vesicles 'steal' amphiphiles from relaxed ones to relieve membrane tension, suggesting that cells that accumulate solutes would grow at the expense of less active cells [7].

The top-down approach, stripping down an existing cell to a minimal set of parts, has traditionally been less powerful for understanding the early origins of life, because life as we know it today is a complicated system of interconnected parts. Although the modern cell presumably evolved from a very simple chemical system through a series of intermediate forms, the last ~3.5 billion years of evolution have optimized the system as a whole and probably obscured most traces of early events. Conventional wisdom and experience have argued that removing genes beyond a minimal subset would kill the cell, preventing the study of less complex life forms. A recent study by Leaver *et al.* [8] begins to dispel this perception, demonstrating that disabling two fundamental processes previously thought to be essential in the bacterium *Bacillus subtilis*, cytokinesis and cell-wall synthesis, nevertheless yields a viable, reproducing organism.

Cell division in bacteria generally proceeds through the formation of a contractile ring composed of the protein FtsZ (the Z-ring), to which other components of the division machinery are recruited. This ring contracts in concert with the synthesis of a new cell wall that separates the two daughter cells. Leaver *et al.* [8] generated a mutant strain of *B. subtilis* that consistently lacked cell walls (L-form bacteria), characterized by an amorphous appearance and large cell size compared with the wild-type strain. Survival of the L-forms was not unexpected, because they can also be generated by exposure to certain antibiotics (for example, penicillin), and some bacteria, such as mycoplasma, naturally lack cell walls. Cell division of L-forms, however, was assumed to involve the Z-ring. Remarkably, when FtsZ was deleted from the L-forms, the cells were largely unaffected and continued to grow and divide, indicating that neither the contractile ring nor the cell wall are necessary for cell division [8].

How do these cells divide without a Z-ring or cell wall? As the authors suggest, it is possible that other biological mechanisms are at work, such as actin homologs that form a cytoskeleton, or chromosome segregation that actively drags the nucleoids apart [8]. But could physical mechanisms alone explain cell division? In model protocells, division can occur through simple shearing, which is routinely accomplished in the laboratory [5], and the morphology of large vesicles covers a particularly rich landscape of dynamic and often unexpected forms.

One of the common modes of cell division observed by Leaver *et al.* [8] was the gradual appearance of a long protrusion from the main body of the cell, which then resolved rapidly into several round progeny cells. This pattern is strikingly similar to the 'pearling instability' seen in lipid vesicles, an analog of the well-known Rayleigh instability of fluid cylinders, in which a thin stream separates into droplets to reduce surface area while conserving volume (a dripping faucet, for example). Pearling in tubular membranes can result from a number of different stimuli that create tension